



Avifaunal disarray due to a single despotic species

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ABSTRACT

Aim Reports of profound changes in species assemblages brought about by the influence of strongly interacting species are increasingly common. Where these strong interactors are sensitive to anthropogenic habitat changes, relatively small alterations in the environment can result in large and pervasive shifts in assemblages. We review the evidence for widespread assemblage-level phase shifts across eastern Australia, triggered partly by anthropogenic habitat alteration and mediated by a native, despotic bird: the noisy miner *Manorina melanocephala*.

Location Eastern Australia.

Methods Based on the literature, we developed conceptual models of factors affecting site occupancy by, and ecosystem-level effects of, the noisy miner. We also analysed recent trends in the reporting rate of the noisy miner across its range.

Results Individuals of this species cooperate to aggressively exclude almost all smaller bird species from the areas they occupy. The noisy miner is advantaged by habitat fragmentation and structural simplification—habitat changes that facilitate detection and interception of potential competitors by miners. We report that the species is increasingly prevalent, particularly close to forest and woodland edges. Such edges have mainly been created by human land use. The evidence we reviewed showed: (1) strong causal links between the noisy miner and depressed richness and abundance of smaller birds, particularly nectarivores and insectivores; (2) moderate evidence of a positive association with larger bird species; (3) reduced tree condition stemming from impaired control of insect herbivore populations by smaller insectivores; and (4) a plausible negative effect on plant reproduction through reduced tree condition, altered pollination services and altered seed dispersal.

Main conclusions This is the first synthesis to document the causes and likely ecological consequences of increasingly prevalent phase shifts catalysed by a despotic species on ecosystems at very large spatial scales (> 1 million km²). Native species affected by human activities can become agents that induce ecological dysfunction.

Keywords

Ecosystem disruption, interspecific competition, keystone species, landscape modification, phase shift, strong interactor.

INTRODUCTION

Individual species exert unequal influences on the composition of ecological assemblages. Species that exert far more

influence than would be predicted from their relative biomass have been labelled 'keystone' species (Paine, 1969) or more generally 'strong interactors' (MacArthur, 1972; Menge *et al.*, 1994). Their effects involve a variety of mechanisms

including predation (Menge *et al.*, 1994; Letnic *et al.*, 2009), parasitism (Robinson *et al.*, 1995), habitat transformation (Naiman *et al.*, 1996) and competition (Piper & Catterall, 2003). Strong interactors can increase (Brown & Heske, 1990) or depress (Colgan, 1987; Horsley *et al.*, 2003) assemblage diversity, potentially shifting assemblages to alternative states that can be difficult to reverse (Suding *et al.*, 2004). For example, local extinctions and reductions in species diversity caused by the cascading effects of humans introducing non-native predators into island ecosystems (Holdaway, 1999; Short *et al.*, 2002; O'Dowd *et al.*, 2003) or extirpation of keystone predators (Wilcove, 1985; Crooks & Soule, 1999; Rooney & Waller, 2003) are well documented.

An assemblage-level shift mediated by a strong interactor can be either a switch between alternative ecosystem states that can exist in a given set of environmental conditions, or a phase shift. A phase shift is a shift in an assemblage brought about by the exploitation of environmental change, particularly by strong interactors (Donahue *et al.*, 2011). The catalyst for such phase shifts, although mediated through the actions of a strong interactor, often is anthropogenic land use change. In this way, even native species affected by human activities have become agents that induce ecological dysfunction. For example, habitat fragmentation associated with human land uses has resulted in increased permeation of forest habitat by some avian nest parasites and predators, and the consequent decline in reproductive success has been implicated in altered structure of forest bird assemblages in North America (Robinson *et al.*, 1995). Altered forest structure and local extinction of native predators have resulted in increased populations of white-tailed deer *Odocoileus virginianus* Z., which act as keystone herbivores, profoundly altering both plants and bird assemblage structure across the eastern United States (Waller & Alverson, 1997).

Although the primary mechanisms in many cases involve predatory or parasitic interactions, assemblage-level effects may also be mediated by competitive interactions with indigenous species that have benefited from human actions. Despotic habitat selection is the process whereby one species, usually the physically larger species, occupies the more-productive habitats to the exclusion of subordinate species (Fretwell & Lucas, 1970; Robinson & Terbourgh, 1995). This mechanism has been identified in groups as diverse as Amazonian birds (Robinson & Terbourgh, 1995), Tibetan snowfinches *Montifringilla* spp. (Zeng & Lu, 2009), desert rodents (Brown & Munger, 1985) and coral reef fishes (Shulman, 1985), but usually has been explored for its role in determining spatial segregation of similar species. The potential for anthropogenic habitat alteration to interact with competitive despotism and affect the structure of entire assemblages has received little attention.

We review the evidence for widespread assemblage-level phase shifts, triggered partly by anthropogenic habitat alteration and mediated by a despotic species (*sensu* Mac Nally *et al.*, 2000). The strong interactor is the noisy miner *Manorina melanocephala* Latham. This medium-sized (63 g)

passerine bird is widespread over 1.3 million km² of eastern Australia (Higgins *et al.*, 2001). Also referred to as a 'reverse keystone' species (Piper & Catterall, 2003), the noisy miner aggressively excludes almost all small-bodied bird species (< 50 g) from its territories, with large effects on the composition and diversity of entire bird assemblages (Dow, 1977; Loyn, 1987a; Piper & Catterall, 2003; Mac Nally *et al.*, 2012). Furthermore, increased incidence (and hence effect) of the noisy miner has been attributed to anthropogenic habitat changes such as forest and woodland fragmentation (Loyn, 1987a; Clarke *et al.*, 1995; Ford *et al.*, 1995; Mac Nally *et al.*, 2000; Major *et al.*, 2001a; Piper & Catterall, 2003). This species' wide distribution, large effect on other birds and positive response to anthropogenic landscape change are a potent combination with the attendant risk of widespread ecological effects. However, despite numerous local-scale studies, there has been no broad-scale synthesis of the scale, causes and consequences of the phenomenon.

Here, we present a unified synthesis of the state of knowledge relating to the avifaunal and broader ecosystem-level disruption mediated by the noisy miner. Based on the literature, we build two conceptual models, and we present a summary of evidence for their component processes. The first model ('occupancy model') considers how anthropogenic and natural factors contribute to the occupancy of sites by the noisy miner. The second model ('effects model') considers how noisy miner occupancy affects other bird species, and how consequent effects may cascade through ecosystems. We also identify important areas of uncertainty, and present a new analysis of the noisy miner's geographical occurrence patterns and its temporal trends.

SITE OCCUPANCY BY THE NOISY MINER

Noisy miner behaviour

The noisy miner is an obligate cooperative breeder that lives in aggregations of up to several hundred birds (a 'colony'), each of which comprises one or more 'coteries' that themselves comprise multiple abutting home ranges belonging to breeding females with several associated males (Dow, 1979; Poldmaa *et al.*, 1995; Higgins *et al.*, 2001). Groups of differing size (which may include members from multiple adjacent coteries of a colony) act cooperatively to attack, chase and, where possible, expel a wide range of species (avian, mammal and reptile) from the colony's territory (Dow, 1977; Clarke, 1984).

Occupancy model

The noisy miner occupancy model (Fig. 1) considers the probability that a given site becomes an 'interspecific exclusion zone', or IEZ – a part of a colony's territory that is actively defended by the noisy miner. The noisy miner can become abundant and dominant in both continuous and fragmented forest and woodland, and in suburban areas. The

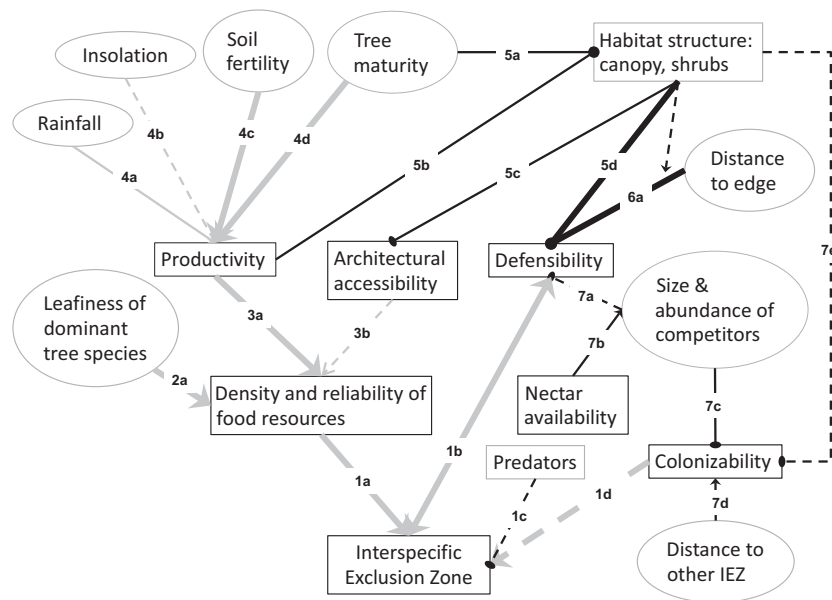


Figure 1 The 'occupancy model': the conceptual model of the interspecific exclusion zone (IEZ). See Supporting Information Table S1 for pathway details and supporting references. Grey lines with arrows = positive influence; black lines = negative influence; bold/faint line = strong/weak influence; dashed lines = hypothesized pathway for which evidence currently is relatively weak.

woodland sites that the miner occupies tend to be those most altered through grazing by livestock, removal of understorey, thinning of trees or, in fragmented landscapes, the introduction of wooded-agricultural edges and narrow corridors of trees (remnant or replanted) (Loyn, 1987a; Catterall *et al.*, 1997, 2002; Major *et al.*, 2001a; Martin & Possingham, 2005; Hastings & Beattie, 2006; Martin *et al.*, 2006; Martin & McIntyre, 2007). The noisy miner also occupies urban and suburban habitats, including inner city parks, suburban gardens and bushland remnants (Sewell & Catterall, 1998; French *et al.*, 2005; Daniels & Kirkpatrick, 2006; Parsons *et al.*, 2006; Ashley *et al.*, 2009). Various forms of anthropogenic vegetation change appear to have triggered much elevated abundances of the noisy miner within its natural range (Ford *et al.*, 1995, 2001; Robinson & Traill, 1996; Recher, 1999; Olsen *et al.*, 2005; Eyre *et al.*, 2009). However, the environmental correlates of occupancy are complex, and there are numerous exceptions: small and degraded remnants of certain vegetation types are often not colonized by the noisy miner [e.g. *Callitris* and *Allocasuarina* forests and woodlands, some *Eucalyptus camaldulensis* Denh. floodplain forests and some shrubby dry *Eucalyptus* woodlands (Major *et al.*, 2001a; Maron, 2007; Kath *et al.*, 2009)] while some very large (> 1 million ha) and relatively intact expanses of woodland are dominated by the noisy miner (Howes & Maron, 2009). We aimed to reconcile these apparent inconsistencies.

In spite of such geographical difference in site-specific environmental determinants of the IEZ, we hypothesize that the proximate habitat requirements of the noisy miner are relatively consistent throughout the species' range. Thus, the IEZ model has a hierarchical structure based on three main

factors: food resources, defensibility and colonizability (Fig. 1). We briefly describe each element below (See Table S1 in Supporting Information for full descriptions of model pathways).

Food availability and stability

The high density of individuals in noisy miner colonies and the species' energetically expensive territorial defence behaviour mean that plentiful food resources must be available year-round as a condition for site occupancy. The noisy miner belongs to the avian family Meliphagidae (honeyeaters) whose species typically feed on a mix of insects, nectar and fruit (Higgins *et al.*, 2001). Although meliphagid species are mainly nectarivorous and typically must move large distances to track flowering patterns (Woinarski *et al.*, 2000), the noisy miner is sedentary. Sites with local year-round availability of nectar are uncommon, so noisy miners depend on invertebrate prey, together with a source of carbohydrate such as nectar or lerp (the sugary secretions of psyllid insects) (Higgins *et al.*, 2001; Ashley *et al.*, 2009). Where the dominant tree species is wind-pollinated and/or has very small or needle-like leaves, nectar and folivorous invertebrate availability generally are inadequate to support a colony (Hastings & Beattie, 2006; Maron, 2007).

Although flexible in its foraging behaviour, the noisy miner is predominantly a foliage gleaner (Maron, 2009). Foliage-dwelling arthropods are often more abundant in the fertile parts of the landscape (Major *et al.*, 2000), and the noisy miner frequently is associated with these more-productive areas, avoiding elevated, rocky, infertile and drier parts of the landscape where food resources may be less consistently

available (Oldland *et al.*, 2009). The native vegetation of more-productive soils has been cleared preferentially for agriculture, creating a landscape pattern in which the edges of large patches of remnant woodland are on more fertile soils than are the interiors (Hobbs & Hopkins, 1990). Edge habitats are also likely to be more productive as a consequence of trapping wind-borne nutrients (Weathers *et al.*, 2001). Therefore, woodland edges commonly coincide with more-productive habitat for the noisy miner, and this correspondence potentially contributes to the species' preference for small woodland patches and edge habitat in some regions (Oldland *et al.*, 2009).

Defensibility

The noisy miner invests substantial time and energy expelling intruders from the IEZ, so structural and spatial factors that affect the efficiency with which a colony can defend its territory are likely to be important. In sites with low vegetation density, intruders are more visible and less able to find refuge from attack. Expelling small birds from sites containing a dense foliage stratum is likely to cost more in time and energy, and be less effective. Many studies have noted the noisy miner's preference for more open forests and woodlands, including those where the understorey has been thinned or removed by livestock grazing, fire, or mechanical clearing, and its absence from more structurally complex sites (Sewell & Catterall, 1998; MacDonald & Kirkpatrick, 2003; Maron & Kennedy, 2007; Howes & Maron, 2009; Montague-Drake *et al.*, 2011).

In more structurally dense habitats such as forest, noisy miner colonies occur more frequently on edges adjacent to, or protrusions into, open country such as urban or agricultural land, especially where there are adjacent scattered trees or suitable suburban-style gardens (Loyn, 1987a; Piper & Catterall, 2003; Taylor *et al.*, 2008). These configurations increase the visibility of approaching birds and reduce the frequency of intruders approaching the territory (Belisle & Desrochers, 2002; Robertson & Radford, 2009). There seems to be no preference for edges in the open, grassy woodlands of the continent's north (Howes & Maron, 2009) where visibility is high even within continuous woodland.

Colonizability

Apparently-suitable sites may remain unoccupied by noisy miners if the site is distant from potential sources of colonists, or if the process of colonization (and expulsion of potential competitors) would be too costly. The triggers for a colony to establish on a new site are unknown, but may include the density of competitors relative to the productivity of the site and a site's defensibility by noisy miners (Mac Nally & Timewell, 2005; Taylor *et al.*, 2008). During a recent 13-year drought (Kiem & Verdon-Kidd, 2010), occurrence of small woodland birds in southern Australia decreased markedly, accompanied by a decrease in the density of vegetation,

while noisy miners increased (Mac Nally *et al.*, 2009). This climate trigger potentially leads to hysteresis, in which once there is colonization by the noisy miner, a return to the original climatic and environmental conditions may not result in a reversal of the phase shift if small birds are prevented from recolonizing. One account of colonization involved groups of ≥ 6 noisy miners moving progressively through adjacent canopy trees in woodland, expelling all other bird species from each tree as the miners progressively gained control of an expanding territory (Clarke, 1984).

DISTRIBUTION AND TEMPORAL TRENDS

Given the probable role of anthropogenic habitat change in facilitating the domination of sites by the noisy miner, it is likely that the species has become more prevalent among regions affected by recent human land uses. While there is little evidence of range expansion, reporting rates (numbers of occurrences as a proportion of numbers of surveys) in several bioregions [based on the Interim Biogeographical Regionalization for Australia (Thackway & Cresswell, 1995)] increased between the early 1980s and the late 1990s (Barrett *et al.*, 2003). There were substantial increases in noisy miner abundance in suburban Brisbane between the early 1990s and mid-2000s (Catterall *et al.*, 2010), while abundance in adjacent forest remained unchanged. There was a doubling in noisy miner density in the Barraba region of central New South Wales between the mid-1990s and early 2010s (D.L. Oliver, unpublished data).

To evaluate recent trends in the reporting rate of the noisy miner across its range, we analysed the BirdLife Australia Atlas dataset for trends in reporting rates between 1998 and 2012, using data from 69,718 surveys from 51,980 sites in 37 bioregions (Fig. 2a). We used a Bayesian mixed effects model with spatially structured random intercepts and slopes to estimate overall and bioregion-specific trends in noisy miner reporting rates (= probability of detection within a standard 2 ha, 20 min survey). The model included nonlinear effects of distance to woodland edge with interactions between time and distance-to-edge, and nested random intercepts corresponding to site, subregion and bioregion scales to account for spatial variation that might otherwise confound trend estimates (full model details are listed in the Supporting Information Appendix S1). This analysis revealed substantial evidence ($> 90\%$ posterior probability of change) for increased noisy miner reporting rates in nine bioregions and evidence for decreases in none (Fig. 2a,b). Increases were confined mainly to woodland edges and non-woodland areas, with reporting rates in woodland interiors remaining similar throughout the survey period in most areas.

A MODEL OF ECOSYSTEM EFFECTS

The effects model (Fig. 3) represents the range of known or very probable ecological effects of the noisy miner (for full details of model pathways see Table S2). The most thoroughly

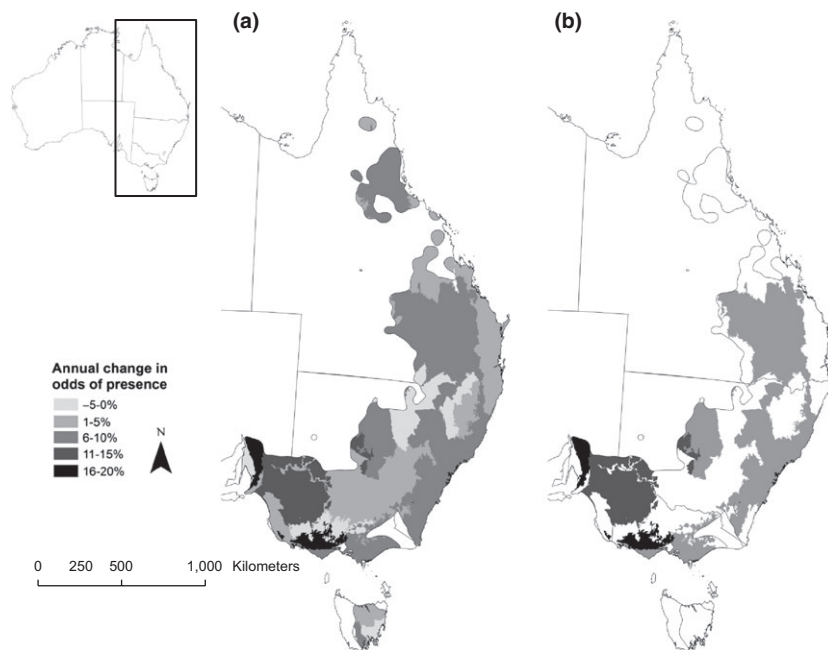


Figure 2 Results of analysis of trends in noisy miner reporting rate based on BirdLife Australia Atlas data within the species' distribution between 1998 and 2012. (a) shows the posterior mean estimate of the annual change in odds of noisy miner presence at sites in all bioregions; (b) shows the estimate for only those bioregions for which there was substantial evidence of an increase (> 90% posterior probability of change) in reporting rate.

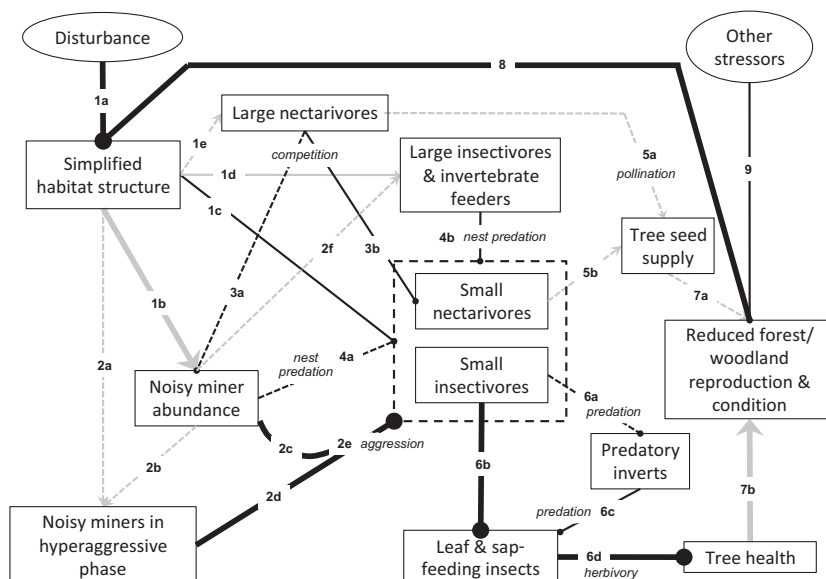


Figure 3 The 'effect model': conceptual model demonstrating the pathways through which the noisy miner may influence ecosystems. See Supporting Information for pathway details and supporting references. Grey lines with arrows = positive influence; black lines = negative influence; bold/faint line = strong/weak influence; dashed lines = hypothesized pathway for which evidence currently is relatively weak.

documented effect is on the richness and abundance of smaller passerine bird species (Dow, 1977; Loyn, 1987a; Grey *et al.*, 1997, 1998; Major *et al.*, 2001a; Piper & Catterall, 2003; Maron *et al.*, 2011). However, substantial shifts in bird assemblage structure linked to domination by the noisy miner are likely to

have cascading effects through to other trophic levels, and, ultimately, upon the state of the vegetation. In this section, we first review the effects of noisy miner occupancy on the avifauna (subdivided into two major functional groups containing large-bodied and small-bodied species), and then

we review the mechanisms of consequent effects on ecosystem processes, with emphasis on herbivory and tree condition, and pollination and seed set.

Effects on avifaunas

Small insectivores and nectarivores

The noisy miner appears to cause substantial reductions in small birds in remnant forest and woodland. In landscapes or vegetation types in which the noisy miner is scarce or absent, even small or degraded remnants may be used by a wide range of birds from distinct guilds with different sizes, bill shapes and feeding ecologies (Oliver *et al.*, 1999; Fischer & Lindenmayer, 2002; Maron, 2007). Grey and colleagues (Grey *et al.*, 1997, 1998) tested the effects on avian diversity and abundance of removing the noisy miner from small (< 10 ha) woodland remnants. These experimental removals were followed rapidly by an influx of small, mobile insectivorous birds, thus providing evidence that when densities of the noisy miner are reduced, many small birds use even degraded woodland remnants for nesting and feeding in the absence of changes in environmental conditions (Grey *et al.*, 1997, 1998). Most of the bird species excluded are smaller in body mass than the noisy miner (i.e. < 63 g), and most are insectivores or nectarivores (Piper & Catterall, 2003; Parsons *et al.*, 2006; Mac Nally *et al.*, 2012). Relative body size is frequently the factor that determines competitive superiority in interspecific interference competition (Schoener, 1983; Persson, 1985; Brown & Maurer, 1986), and the cooperative behaviour of noisy miners may enhance the species' effectiveness in excluding other species.

There are additional pathways (other than the noisy miner's agonistic behaviour) through which small birds may be affected. Domination of sites by the noisy miner is associated with an increase in the density of predators of eggs, nestlings and small adult birds, such as corvids *Corvus* spp., butcherbirds *Cracticus* spp. and currawongs *Strepera* spp. (Maron & Kennedy, 2007). While shared habitat preferences may contribute to this association, butcherbirds appear to be tolerated by the noisy miner and the species cooperate in antipredator responses (Maron, 2009). In one case, this association appeared to result in the death of a newly translocated brown treecreeper *Climacteris picumnus* Temm. & Laug. from a butcherbird attack (Bennett *et al.*, 2012). A similar association with butcherbirds has been reported for the yellow-throated miner *Manorina flavigula* Gould, a congener of the noisy miner with similar social structure and aggressive behaviour (Fulton, 2008). Mutual benefits could arise from these associations if combined efforts lead to improved defence and increased food supplies for the miners and the larger-bodied birds. Piper and Catterall (Piper & Catterall, 2004, 2006) implicated both the noisy miner and butcherbirds in higher artificial nest predation at woodland-agricultural edges, suggesting the potential for both direct and indirect roles of the noisy miner in increased nest predation.

Large nectarivores, insectivores and vertebrate feeders

Sites that are dominated by the noisy miner are usually occupied mainly by larger bird species, such as large-bodied nectarivores (wattlebirds *Anthochaera* spp., friarbirds *Philemon* spp. and lorikeets (parrots) *Trichoglossus* spp. and *Glossopsitta* spp.), granivores (large parrots Psittaciformes and doves Columbidae) and carnivores (especially butcherbirds). This pattern is due not only to the absence of small birds but to a positive association between the noisy miner and some larger-bodied species (Major *et al.*, 2001b). It is less clear whether the tendency for larger species to be more common in sites with high densities of the noisy miner is causal because many larger-bodied species may prefer the more-degraded sites that the noisy miner frequently occupies. The noisy miner often occupies the more nectar-rich parts of the landscape (Major *et al.*, 2001a), where they are more likely to co-occur with the large-bodied nectarivores that tend to resist or ignore miner attack (French *et al.*, 2005; Maron, 2009).

Effects on ecosystem processes

Insect herbivory and tree health

The exclusion of small insectivorous birds by the noisy miner may exacerbate dieback of tree canopies caused by high densities of foliage-eating insects in small woodland remnants (Ford & Bell, 1982; Loyn, 1987a). Severe defoliation by insects and subsequent dieback may be common in small, heavily grazed remnants (< 10 ha) occupied by the noisy miner (Loyn, 1985, 1987a). MacDonald & Kirkpatrick (2003) found that sites dominated by the noisy miner had higher levels of tree dieback than did sites where noisy miner density was low. There was steady improvement in tree condition following the experimental removal of the noisy miner in small, degraded remnants, which was greater than that in remnants where the noisy miner remained (Grey, 2008).

Pollination and seed set

Many tree and shrub species of Australian forests and woodlands are pollinated by birds (Ford & Paton, 1986). Most nectarivorous birds are highly mobile (McGoldrick & Mac Nally, 1998; Woinarski *et al.*, 2000), but the territorial and sedentary nature of the noisy miner limits the distances over which its own nectar feeding can facilitate pollen flow. Wide-ranging avian nectarivores in woodland dominated by the noisy miner are mainly large honeyeaters and nectarivorous parrots. Large honeyeaters frequently defend feeding trees (Woinarski *et al.*, 1997). Small honeyeaters move more frequently between trees and are more effective pollinators (House, 1997), but most are excluded from noisy miner territories. The miner-associated change in the pollinator profile of affected woodlands is likely to reduce the efficacy of pollination and gene flow, at least for some trees and shrubs. The consequent pollination limitation and reduced seed set and

quality are likely to affect the long-term health of woodlands (Paton, 2000; Southerton *et al.*, 2004).

DISCUSSION

Progress towards a synthesis

This review is the first synthesis of phase shifts triggered by a despotic species on ecosystems at very large spatial scales (> 1 million km²). We document a syndrome of avifaunal disarray accompanied by disruption of ecosystem processes that could result in irrevocable loss of species and habitats across over a third of a continent. To our knowledge, no single species acting within its native range has been found to restructure entire assemblages to such an extent.

While many details of the component processes are yet to be clarified, and may differ among regions within the noisy miner's range, the main strands of argument are well supported. The influence of the noisy miner on smaller bird species is evident whenever a minimum density of the noisy miner was present regardless of the vegetation type or its condition (Mac Nally *et al.*, 2012). In the Interspecific Exclusion Zone (IEZ) created by territorial defence in noisy miner colonies, there is a change in the insectivore and nectarivore assemblage from one with diverse bird sizes, bill shapes and movements to a more homogeneous assemblage dominated by sedentary, large-bodied species and large-billed species (Mac Nally *et al.*, 2012).

Although the direct influence of the noisy miner on smaller birds is unequivocally supported, the cascading effects of the avifaunal consequences have been less thoroughly documented. The exclusion of small-bodied insectivores and nectarivores is likely to narrow the range and reduce the provision of insect predation and pollination by birds. The association between the noisy miner and tree dieback from insect herbivory is not strongly established [although see Grey (2008)], but experimental reduction in the congeneric bell miner *Manorina melanophrys* Latham, a similarly despotic species, led to reduced insect populations, and sometimes to improved tree condition (Loyn *et al.*, 1983; Loyn, 1987b).

Targeted work on the influence of noisy miners on pollination dynamics is needed. Changes in rates of pollination or seed set in plants from noisy miner-mediated phase shifts have not been established, but it is plausible that the different avian foraging guild composition in noisy miner-dominated sites results in at least altered patterns of pollination. A change in the nectarivore assemblage from one with diverse bird sizes, bill shapes and movement strategies to a more homogeneous assemblage dominated by less-mobile, large-bodied species predictably occurs within the IEZ (Mac Nally *et al.*, 2012). Many trees and shrubs in eucalypt forest and woodland are bird-pollinated (Paton, 2000), and so a nectarivore assemblage that is dominated by a few larger species that move among fewer trees while foraging is likely to result in reduced outcrossing and consequently

reduced seed set and compromised seed quality (Paton, 2000; see also Table S2), with longer-term implications for plant recruitment.

The model of the IEZ essentially incorporates: (1) the availability and variability of food resources; (2) defensibility of a site; and (3) site colonizability, with the environmental factors typically found to be correlates of site occupancy driving site suitability through their influence on one or more of these three factors. This hierarchical approach reconciled inconsistent results about whether the noisy miner preferentially occupies edge habitats. For example, no preference for edges was evident in a study of open, grassy woodlands (Howes & Maron, 2009), whereas edge preference has been observed in studies from other regions with denser vegetation (Piper & Catterall, 2003; Clarke & Oldland, 2007). The IEZ suggests that the defensibility of a site in denser vegetation is likely to be increased if surveillance is enhanced by an edge position. Where the noisy miner is absent from small patches of woodland of apparently suitable vegetation structure (Maron, 2007), factors linked to food availability and stability may be responsible. For example, where the dominant tree species is wind-pollinated and/or has very small or needle-like leaves, both nectar and the availability of folivorous invertebrates may be inadequate to support a colony (Hastings & Beattie, 2006; Maron, 2007).

Why is the disarray worsening?

Increases in the prevalence of the noisy miner in recent decades may be due to several factors. First, anthropogenic modification of both the structure of vegetation at a site and the configuration of native vegetation in the landscape changes habitat suitability for the noisy miner in potentially complex ways. While the clearing and fragmentation of remnant vegetation have meant that edge habitats suitable for noisy miners now pervade many landscapes (Oldland *et al.*, 2009), the scattered paddock trees that increase the probability of noisy miners occupying adjacent woodland (Taylor *et al.*, 2008) are also being lost through intensification of agriculture (Maron & Fitzsimons, 2007; Manning *et al.*, 2013). Frequent fire and grazing may help create open habitat (Howes *et al.*, 2010), but fire can also encourage dense regrowth that is unsuitable for noisy miners (Grant, 2003).

Second, some of the increase in noisy miner abundance may be attributable to changes in climate. There was a decline in about two-thirds of woodland bird species during a 13-year drought (1997–2010) in Victoria, but the noisy miner became more abundant (Mac Nally *et al.*, 2009). Conditions have been hotter and drier than the long-term average over the past 20 years in south-eastern Australia, potentially facilitating noisy miner colonization through altering vegetation structure; there is strong evidence of reduced canopy and shrub cover between 1998 and 2011 (Bennett *et al.*, 2013).

Third, the increasing prevalence of noisy miners is also likely to be time-lagged, resulting from habitat change (land

clearing) that occurred several years to many decades ago. The life histories of Australian passerines, notably co-operative breeders such as the noisy miner, are characterized by low reproduction and high adult survival (Russell & Rowley, 1993; Clarke, 1995). Noisy miners are also highly sedentary and slow to colonize new habitat patches, so that, given the continuation of current land use patterns over time, noisy miners will probably colonize more of the modified woodland of eastern Australia.

Dynamics of despotic-driven ecosystem disruption in human-modified landscapes

Although the effects of human-induced alterations of the landscape can be obvious (e.g. habitat loss), other effects may be more subtle and produce complex disruptions of interactions among species. While many species have declined in distribution and abundance with habitat loss and fragmentation (Ford *et al.*, 2001; Butchart *et al.*, 2010), some native species have increased in abundance and distribution in human-modified landscapes (Lunney *et al.*, 2007), and some of these are implicated in unexpected negative effects on the rest of the biota (Recher & Lim, 1990; James *et al.*, 1999). These occurrences are just as much a sign of ecosystem dysfunction as are species' declines and extinctions (Noss, 1990; Garrott *et al.*, 1993; Recher, 1999).

Although the noisy miner is an extreme case of assemblage disruption by one native species, in the context of rapid global change, the phenomenon is not just an Australian 'oddity'. Many of the factors that predispose habitats to occupancy by the noisy miner are common consequences of human-caused landscape alteration. The brood parasitic brown-headed cowbird *Molothrus ater* Bodd. responded positively to increases in open grazing land and the fragmentation of forest in North America. Such landscape modification enabled this open-country species to penetrate into remnant forest, and the consequent elevated rates of nest parasitism threaten the persistence of forest-dependent passerines (Robinson *et al.*, 1995).

Systems subject to strong interactions among their component species are considered to be particularly vulnerable to the impacts of disturbance (Suding & Hobbs, 2009). Accordingly, where strong interactors are sensitive to anthropogenic habitat modification, small alterations in the environment can result in large and pervasive changes in assemblages, and the resultant assemblage may persist even if the initial perturbation is reversed (Scheffer & Carpenter, 2003; Mac Nally, 2008; Blackwood *et al.*, 2012). In the case of the noisy miner, this would mean that once a colony is established, environmental manipulations alone may be inadequate to reverse the phase shift.

Species that are strong interactors are potentially serious threats to biodiversity if widely established beyond their native range. However, accidental introduction of the noisy miner, leading to its establishment outside Australia, seems unlikely because of its colonial and cooperatively breeding

habits, and because it is not favoured by aviculturists. Nevertheless, *Eucalyptus* plantations may plausibly provide suitable habitat for the noisy miner; such plantations occur increasingly widely around the world, and even though this genus is not currently considered highly invasive, some eucalypt species have spread extensively beyond the original plantations (Booth, 2012). The accidental establishment and spread of the noisy miner would likely have severe consequences for a naïve avifauna.

The syndrome of avifaunal disarray that we have described in this study has intensified in response to anthropogenic disturbances that are typical of those affecting most terrestrial systems on the planet. There is considerable potential for similar syndromes to arise elsewhere, when species pre-adapted for interspecific territorial behaviours or other influential interactions may come to exert disproportionate influence over the ecosystems they inhabit. We highlight the risk that ongoing changes in climate and land use can cause profound ecosystem disruption not only directly, but also through phase shifts triggered by strongly interactive species, both alien and native.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Occupancy model pathway descriptions, supporting evidence, and level of confidence for each process contributing to the probability of a site being within an interspecific exclusion zone (IEZ).

Table S2 Miner effect model pathway descriptions, supporting evidence, and level of confidence for each process.

References S1 Full references for Supporting Information Tables S1 and S2.

Appendix S1 Details of Bayesian mixed effects model of temporal trends in noisy miner reporting rates.

BIOSKETCH

The noisy miner working group comprises fifteen members from twelve organizations and research institutions across eastern Australia. It aims to develop a synthesis of the anthropogenic and natural factors contributing to the domination of avifaunas by the noisy miner and understand the process of noisy miner invasion. The group is supported by the Australian Centre for Ecological Analysis and Synthesis. This is the first of a series of publications arising from two workshops held during 2012.

Authors contributions: All authors contributed to conceptual model development and manuscript; J.T. and R. Mac Nally conducted the temporal trend analysis.

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